

A NEW SUBFAMILY OF CRETACEOUS ANTLIKE STONE BEETLES
(COLEOPTERA: SCYDMAENIDAE: HAPSOMELINAE) WITH AN EXTRA
LEG SEGMENT

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Abstract.—A new subfamily, genus, and species of antlike stone beetles (Coleoptera: Scydmaenidae: **Hapsomelinae**: *Hapsomela burmitis*) are described from Cretaceous Burmese amber. The forelegs of the fossil contain a patella, the major character on which the new subfamily is based. The patella is regarded as an example of functional morphology and probably served in the capacity of catching and/or holding down prey, probably mites, since all extant members of this family are mite predators. This character appears to have been specific to this clade of antlike stone beetles, since no other members (extinct or extant) of the family have a patella. Another unusual character of *H. burmitis* is the extended abdomen and elongate strongly sclerotized ovipositor, thus allowing eggs to be inserted into cracks or soft tissue. The significance and occurrence of the extra leg segment in this group of beetles is discussed in relation to Paleozoic insects and modern arthropods.

Key Words: Hapsomelinae n. subfam., *Hapsomela* n. gen., *Hapsomela burmitis* n. sp., Burmese amber, Cretaceous, patella

Antlike stone beetles comprise a small, staphylinoid family characterized by elongate elytra, five-segmented tarsi, six visible abdominal sternites, and clavate femora (O'Keefe 1998). They are placed in the family Scydmaenidae Le Conte of the Staphyliniformia, with two subfamilies (Mastiginae Fleming and Scydmaeninae Leach) and 13 tribes (Newton and Thayer 1992). We describe a unique scydmaenid from Burmese Cretaceous amber, which demonstrates fore legs with a patella.

MATERIALS AND METHODS

The amber was recut and polished in order to better view the fossil beetle. The amber piece containing the fossil is trapezoidal in outline, 1 mm in depth, with the sides measuring 5, 3, 6, 1, and 4 mm, respective-

ly. Observations, drawings, and photographs were made with a Nikon Optiphot microscope (with magnifications up to 650 \times).

Amber from Burma occurs in lignitic seams in sandstone-limestone deposits in the Hukawng Valley. Nuclear magnetic resonance (NMR) spectra of amber samples taken from the same locality as the fossil indicated an araucarian (possibly *Agathis*) source of the amber (Lambert and Wu, unpublished research 2002). Palynomorphs obtained from the amber beds where the fossil piece originated have been assigned to the Upper Albian of the Early Cretaceous (100–110 mya) (Cruickshank and Ko 2003).

The amber specimen could not be placed in either of the two subfamilies since it pos-

sessed a pointed labial palpomere 3, a character of the Mastiginae, and antennomere 1 not nearly as long as antennomeres 2–4 combined and antennae not geniculate between antennomeres 1 and 2, both characters of the Scydmaeninae (O'Keefe et al. 1997). In addition, we consider the extra leg segment in the fore legs to be a significant character for the new subfamily.

**Hapsomelinae Poinar and Brown,
new subfamily**

Diagnosis.—A patella in the forelegs separates this subfamily from the other two in the family Scydmaenidae. In addition, labial palpomere 3 pointed; antennae not geniculate; antennomere 1 only slightly longer than antennomere 2; distal antennomere only forms club.

**Hapsomela Poinar and Brown,
new genus**

Type species.—*Hapsomela burmitis* Poinar and Brown.

Description.—With characters listed under subfamily description. Head approximately as broad as long; eyes large, situated behind antennal insertions, widely separated; distal antennomere longest and widest; maxillary palpomere 1 longest; maxillary palpomeres 2–4 approximately equal in length; maxillary palpomere III clavate; abdominal segments protruding beyond tips of elytra, ovipositor enlarged, strongly sclerotized.

Etymology.—*Hapsomela* is from the Greek “hapsos” (feminine) for juncture or joint and the Greek “melos” for limb. The gender is neuter.

***Hapsomela burmitis* Poinar and Brown,
new species
(Figs. 1–8, 10)**

Description.—Holotype female; with characters listed under subfamily and generic diagnoses. Body and legs dark brown, covered with brown setae; body length 1.13 mm. *Head*: Length, 0.38 mm; covered with short erect setae; subocular setae present;

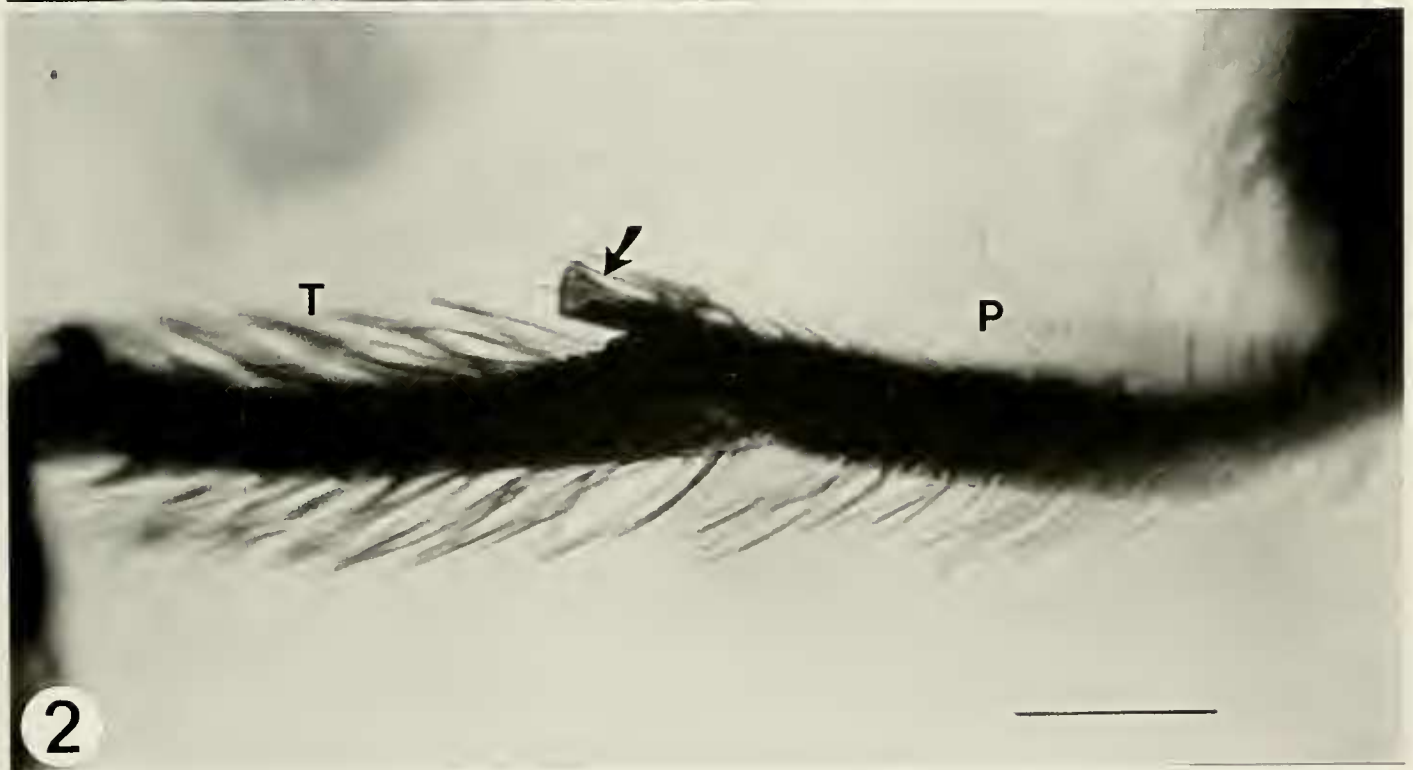
antenna longer than head and pronotum combined, with 11 segments; antennomere I (scape) slightly longer than first antennomere, antennomere II (pedicel) with a few long setae, all other antennomeres densely covered with setae; lengths of antennomeres: 1: 102 μm , 2: 86 μm , 3: 86 μm , 4: 86 μm , 5: 86 μm , 6: 113 μm , 7: 91 μm , 8: 91 μm , 9: 91 μm , 10: 91 μm , 11: 109 μm ; head deflexed; eyes oval, protruding from head margin; mandibles strongly curved, sharply pointed, apparently lacking teeth; maxillary palpomeres elongate, maxillary palpomere I longest, 98 μm ; with following three palpomeres approximately of equal length: 2: 46 μm , 3: 44 μm , 4: 41 μm ; third palpomere thicker than others; labial palpomeres elongate, first palpomere longest, 49 μm ; followed in size by terminal one, 37 μm , with second palpomere shortest, 32 μm ; palpomere III narrow and pointed.

Thorax: Brown, pronotum 380 μm long, almost flat, densely pubescent; legs elongate, slender, inner tips of trochanters bear a blunt tooth; femora long, only slightly clavate; patella with a wide, triangular-shaped spur on inner margin near distal end; front tibia with inner spine and outer blunt spur; meso- and metatibiae without patella; protarsomere lengths as follows: 1: 61 μm , 2: 49 μm , 3: 37 μm , 4: 49 μm , 5: 61 μm , mesotarsomere lengths, 1: 102 μm , 2: 82 μm , 3: 48 μm , 4: 68 μm , 5: 87 μm ; metatarsomere lengths: 1: 159 μm , 2: 85 μm , 3: 66 μm , 4: 54 μm , 5: 88 μm ; claws straight, length, 24 μm on protarsus, 39 μm on mesotarsus, 44 μm on metatarsus.

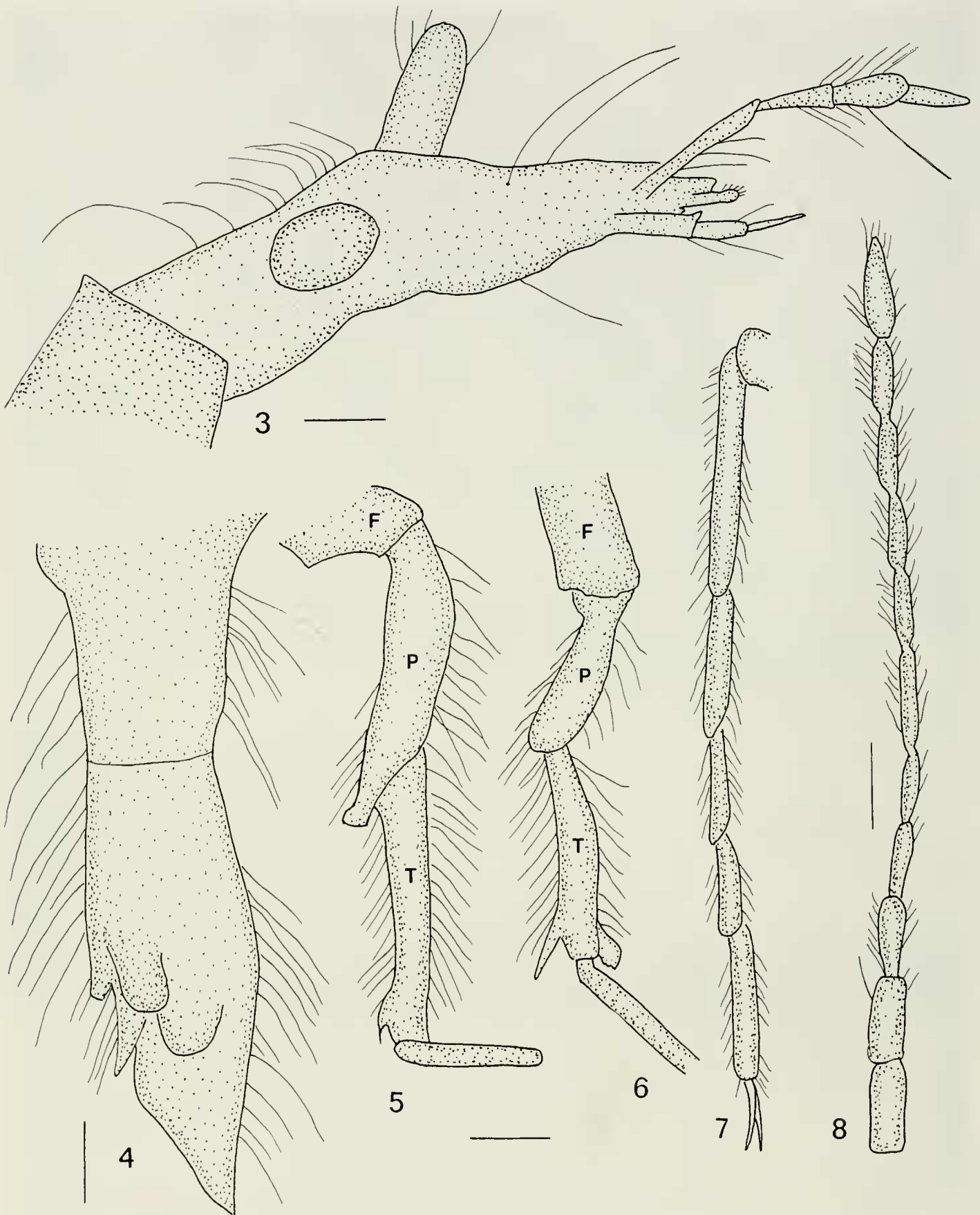
Abdomen: Brown, 415 μm long; scutellum absent, elytra tapered posteriorly, punctate, partially open at apex, with elytral apices bluntly rounded, entire; pygidium exposed, vertical; ovipositor prominent, with triangular protiger, paraprocts and paired valvifers; paired elongate gonocoxae pointed at tip; styli not observed.

Male.—Unknown.

Material examined.—Holotype female in Burmese amber from the Hukawng Valley,



Figs. 1-2. *Hapsomela burmitis* 1. Lateral view of holotype female. Arrow shows joint separating patella and tibia in right front leg. Bar = 345 μ m. 2, Lateral view of right front leg with patella (P) and tibia (T). Arrow shows truncate spur at base of patella. Bar = 77 μ m.



Figs. 3–8. *Hapsomela burmitis*. 3, Lateral view of head with palps. Bar = 48 μ m. 4, Lateral view of ovipositor. Bar = 48 μ m. 5, Lateral view of right front leg. F = femur; P = patella; T = tibia. Bar = 48 μ m. 6, Angled, dorsal (edge) view of left front leg. F = femur; P = patella; T = tibia. Same magnification as Fig. 5. 7, Right metatarsus. Same magnification as Fig. 5. 8, Right antenna. Bar = 90 μ m.

deposited in the Poinar amber collection (accession # B-C-11) maintained at Oregon State University.

Etymology.—The specific epithet *burmitis* is for the country of origin of the fossil.

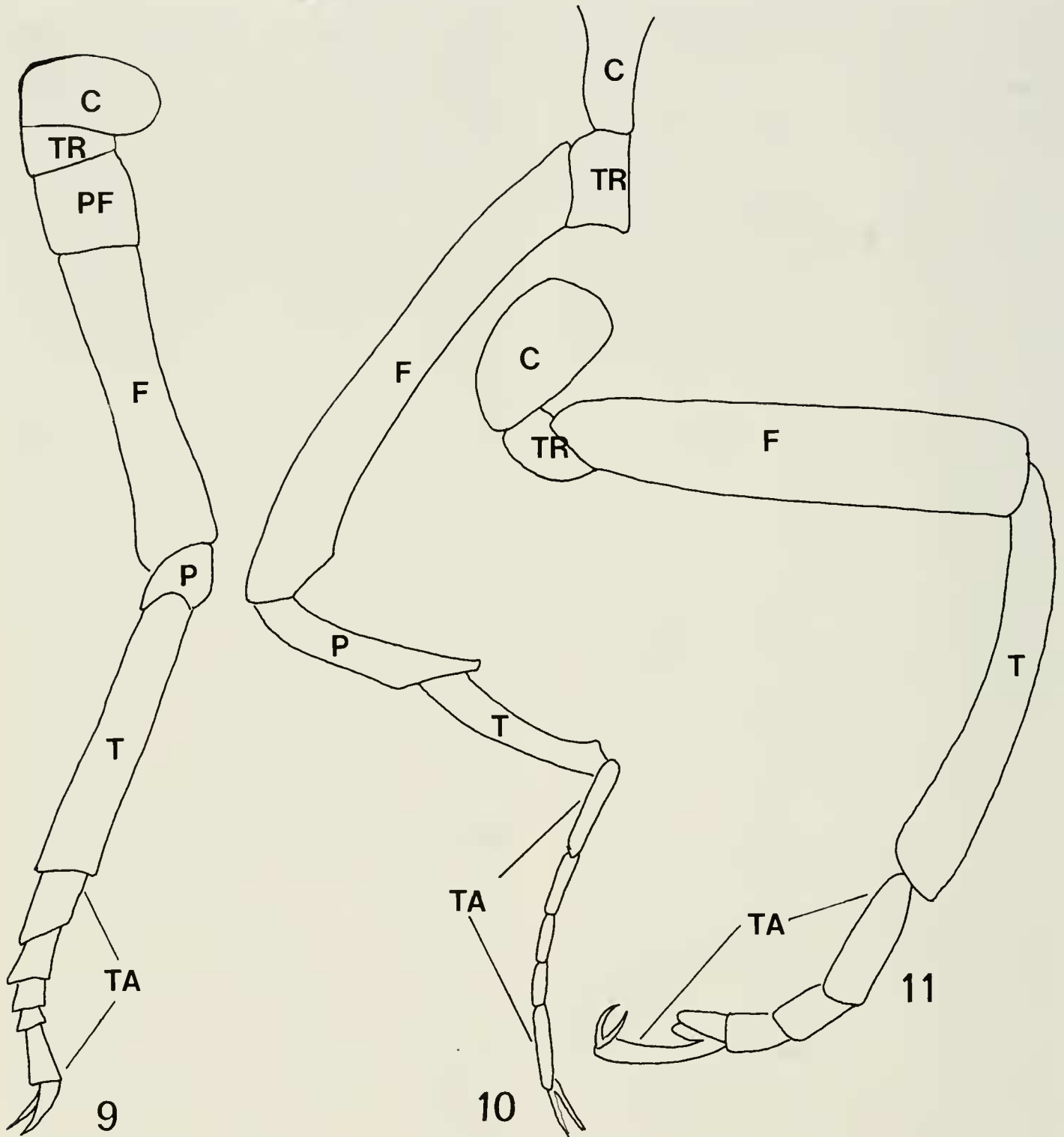
Notes.—In his phylogenetic analysis of the Scydmaenidae, O'Keefe (1998) mentioned a number of additional character states for the family. Those observable in *H. burmitis* are listed below as an addendum to the description and for the benefit of future workers conducting phylogenetic analyses on this group. 1, Vertex approximately as broad as long, with antennal bases slightly separated or vertex distinctly broader than long, with antennal bases widely separated; in *H. burmitis*, the vertex is approximately as broad as long but the antennal bases are widely separated. 2, Maxillary palpomere III subtriangular or elongate; in *H. burmitis*, it is neither of these, but clavate (club-shaped). 3, Elytra free or fused; the elytra in *H. burmitis* are free. 4, Hind wings present or absent; this is difficult to observe in *H. burmitis*, but since the elytra are slightly open at the base, it is assumed that hind wings are present. 5, Elytral punctation deep and distinct, shallow or absent; in *H. burmitis*, the punctation is shallow, but distinct and arranged in rows. 6, Pronotal collar present or absent; it is absent in *H. burmitis*. 7, Pronotum slightly or greatly convex; in *H. burmitis*, it is only slightly convex. 8, Profemoral setae present or absent; in *H. burmitis*, they are absent. 9, Protrochanteral setae present or absent; they are absent in *H. burmitis*, but in their place is a blunt spine. 10, Postgenal setae present or absent: they are present in *H. burmitis*. 11, Maxillary palpomere II with or without bisetose process; it is without in *H. burmitis*. 12, Antennomeres IV–VII slightly longer than wide or 3–5 times longer than wide; they are 3–5 times longer than wide in *H. burmitis*. 13, Maxillary palpomere IV broad, nearly one-third length of palpomere III or elongate, nearly same length as palpomere III; in *H. bur-*

mitis, it is elongate and nearly the same length as palpomere III. 14, Labial palpomere II elongate, parallel-sided or widened medially; it is elongate in *H. burmitis*. 15, Labial palpomere III short or elongate and slender; it is elongate and slender in *H. burmitis*. 16, Antennal insertions widely separated or narrowly separated; they are narrowly separated in *H. burmitis*. 17, Femora strongly or weakly clavate: they are weakly clavate in *H. burmitis*. 18, Elytral striae present or absent; they are absent in *H. burmitis*. 19, Mesotarsomeres I–IV subequal in length or decrease in length; they decrease in length in *H. burmitis*.

DISCUSSION

The main distinguishing character of *H. burmitis* is the presence of a patella on the front legs (Figs. 1, 2, 5, 6, 10). The structure of the patella and a bend at its joint with the left tibia indicates that this is a true dicondylic joint (allowing movement in only one direction) controlled by internal muscles inserted at the base of the anterior protibia, a condition occurring in the legs of most adult insects today (Adler 2003). While insects represent one of the most diverse groups of terrestrial arthropods today, their basic external morphology is fairly conservative. All extant insects possess legs with 5 basic segments, the coxa, trochanter, femur, tibia and tarsus (Fig. 11). The tarsus is usually subdivided into 2–5 additional sub-segments, but together they are still regarded as a single segment. While some extant insects possess secondary segments, such as the trochantellus in some Hymenoptera (Goulet and Huber 1993) and subdivisions of the hind tibia in some caddisfly larvae (Wiggins 1977), no modern or fossil insect from the Tertiary or Mesozoic periods is known to possess more than 5 basic leg segments. However, some insects from the Late Paleozoic do possess extra leg segments, including a patella (Kukalová-Peck 1992) (Fig. 9).

There are three possible scenarios for the presence of this character on *H. burmitis*.



Figs. 9–11. 9, Leg of a Paleozoic paleodictyopteran with two extra joints, a prefemur and patella (modified from Kukalová-Peck 1992). C = coxa; F = femur; P = patella; PF = prefemur; T = tibia; TA = tarsus; TR = trochanter. 10, Foreleg of *Hapsomela burmitis* with patella. C = coxa; F = femur; P = patella; T = tibia; TA = tarsus; TR = trochanter. 11, Leg of extant insect (Coleoptera: Cerambycidae) showing basic 5 segments. C = coxa; F = femur; T = tibia; TA = tarsus; TR = trochanter.

First, this clade of beetles could have carried this feature with them from the Paleozoic, losing the patella in the mid- and hind legs but retaining it in the front legs. Second, the extra segment could have arisen in an early Mesozoic clade that did not have

a patella, but carried the genes responsible for its formation. Or lastly, this character could have arisen as a spontaneous mutation in this particular beetle. The latter scenario seems unlikely since there is no experimental evidence indicating that insects

can spontaneously produce extra leg segments, even with the numerous spontaneous and induced mutations reported in *Drosophila melanogaster* (Lindsley and Zimm 1992). If the expression of an extra leg segment is not feasible by spontaneous mutation (being beyond the possibility of genomic recombination) then it would appear that this condition is either a continual, or resurgent, expression of an ancestral character.

Since extinct Paleozoic forms belonging to the orders Paleodictyoptera, Monura, and Thysanura (Kukalová-Peck 1986, 1992) (Fig. 9), as well as present day myriapods (Barnes 1963), mites (Krantz 1978) and spiders (Comstock 1948), possess patellae, it would appear that the expression of a patella (and other additional segments) is under early developmental control in all arthropods. Unfortunately, the legs of most Paleozoic beetles were not fossilized (Carpenter 1992), and thus it is not possible to know if they had extra leg segments. The present discovery suggests that genes controlling insect leg segments became highly conserved by the Late Cretaceous, thereafter expressing only the 5 basic segments found in extant insects.

All extant scydmaenids feed on mites and use their forelegs to manipulate the prey during feeding (Molleman and Walter 2001, Schmid 1988). The extra leg segment may have been useful in manipulating certain clades of Early Cretaceous mites and was retained for this purpose, making it an example of functional morphology. When this group of mites disappeared, the extra leg segment became useless, or even a hindrance, which would explain the disappearance of this particular beetle clade.

Hapsomela burmitis contains characters found in both the Scydmaeninae and the Mastiginae as well as unique characters not reported previously within the family. One such unique character is the extended abdomen containing the modified ovipositor with a sharp tipped protiger, which would allow the eggs to be inserted into cracks or

soft tissue. When living in a habitat with mites and other small predators, leaving unprotected eggs exposed on the substrate would be risky. Burmese amber is dated at approximately 110–100 mya which would make this specimen the oldest described scydmaenid, some 20–30 million years older than the previously described Cretaceous specimen (O'Keefe et al. 1997).

ACKNOWLEDGMENT

We thank Roberta Poinar for comments on an early draft of the manuscript.

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